Diving behaviour of Atlantic salmon at sea - effects of light regimes and temperature stratification

Running head: Diving behaviour of Atlantic salmon at sea

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ABSTRACT: The diving behaviour of adult Atlantic salmon (*Salmo salar* L.) post-spawners in the Norwegian and Barents Seas was monitored with pop-up satellite archival tags (PSATs) and data storage tags (DSTs). Atlantic salmon from the three populations studied showed similar depth use patterns. Tagged specimens spent most of their time near the surface (mean of 82% of the time at depths <10 m), with occasional short deep dives (>200 m depth, median time = 2.31 h, range = 0.18-22.5 h), the deepest recorded being 707 m. Increased use of greater depths occurred during daytime than night-time in the months between polar day and polar night (August-October). Diurnal behaviour around the time of polar night (November-January) was weakest for the population (from the River Alta) that migrated furthest north. Diving was more frequent and shallower when the mixed layer was near to the surface during the months of June-October. There was an increase in diving depth (>200 m) when the mixed layer extended to ~200-300 m in winter and spring (December-April). Deep diving consisted of ‘U’ shaped dives, possibly indicative of foraging. We hypothesise that seasonal light conditions, dependent on geographical location, affect Atlantic salmon diving, and that changes in diving depth may be due to seasonal differences in prey aggregation.

Key-words Continental shelf, deep sea, feeding, fish, migration, Arctic, North East Atlantic

INTRODUCTION

Atlantic salmon (*Salmo salar* L) are anadromous and undertake oceanic feeding migrations during post-smolt (early adult) and adult post-spawning life-stages (see Dadswell et al. 2010, Miller et al. 2014). They are opportunistic feeders at sea, with their main prey being fish larvae, small epipelagic and mesopelagic fishes, planktonic and large crustaceans, and squid (Hansen & Quinn 1998, Jacobsen & Hansen 2000, Rikardsen & Dempson 2011). In the North Atlantic, Atlantic salmon prey such as herring (*Clupea harengus* L.), sand eels (*Ammodytes* spp.) and amphipods have defined distributions, influenced by the North Atlantic current (Haugland et al. 2006). Thus, the geographic and depth distribution of Atlantic salmon within the North Atlantic may partly reflect that of their prey (Dadswell et al. 2010).

At sea, Atlantic Salmon spend most time in the upper water column, diving aperiodically to greater depths (Jákupsstovu 1988, Lacroix 2013, Strøm et al. 2017). Dives to depths in the excess of 100 m have been observed using telemetry for both post-smolt and post-spawned Atlantic salmon, however, this behaviour appears to be related to the stage of migration and the geographical area (Holm et al. 2006, Lacroix 2013, Godfrey et al. 2015, Gudjonsson et al. 2015). Diving may also be related to foraging and predator avoidance (Reddin et al. 2011). Reddin et al. (2004) proposed a model for energy optimisation by Atlantic salmon involving diving to cold water layers for foraging, and returning to warmer surface waters for digestion. Such thermal regulation has been observed for Pacific Salmon (*Oncorhynchus* spp.) in temperate marine areas, with Chum Salmon (*Oncorhynchus keta*) observed diving into cooler layers, presumably to minimise energy use (Tanaka et al. 2000). However, there would seem to be little advantage to this behaviour in colder northern waters.

In this study, we examined the diving behaviour and activities of adult Atlantic salmon post-spawners in the Norwegian and Barents Seas using individuals from three populations originating from Norwegian Rivers, the Orkla, Alta and Neiden, tagged with either pop-up satellite archival tags (PSATs) or data storage tags (DSTs). We compared long-term (monthly) and short-term (hourly) changes in depth use by individuals from the three populations to examine the influence of light regimes on depth use. We also examined diving for 13 individuals from the Alta population tagged with high resolution DSTs of 1 or 5 minute intervals to examine the influence of light and thermal regimes on diving behaviour.

MATERIALS AND METHODS

Fish telemetry: pop-up satellite archival tags and data storage tags

Adult Atlantic salmon were sampled and tagged in three Norwegian rivers: the Orkla River (63.3°N, 9.7°E), the Alta River (70.0°N, 23.4°E), and the Neiden River (69.7°N, 29.4°E) (Figure 1a). The Orkla and Alta Rivers discharge into the Norwegian Sea through Trondheimsfjord and Altafjord respectively, and the Neiden River discharges into the Barents Sea through Neidenfjord. The Norwegian and Barents Seas are categorised as subarctic/Arctic seas, with sea surface temperatures ranging between ≈15°C in summer and ≈0°C in winter, and thermally stratified waters from July to September/October. Atlantic salmon were caught in the rivers by angling in late April – early May for the Orkla River and mainly from May 10-22 for the Alta and Neiden Rivers (no difference between years in terms of capture time) during their seaward migration period (see Halttunen et al. 2010). Mainly females were retained for tagging as these generally have a higher survival in both the river and sea (Halttunen et al. 2013), but some males were also tagged (≈7% of all tagged individuals). The

Atlantic salmon were kept in storage pens to allow acclimation to sea, before they were anaesthetised for surgery (2-phenoxy-ethanol, 0.5 ml l^{-1}, mean anaesthetising time = 3 min). Each Atlantic salmon individual was cradled in a 25 cm diameter water-filled tube for tagging. The top half of this tube had been removed to enable surgery, but the part surrounding the head of the individual undergoing surgery was kept intact to ensure that light intensity at the individual's eyes was minimised. Water ensured that the head and gills were submerged. Individuals from the Orkla and the Alta rivers were tagged with either a PSAT or a DST, whereas all individuals from the Neiden River were tagged with PSATs (Table 1). All individuals were released between May 3 and June 1.

PSATs (Microwave Telemetry, Inc.) had a mass of 40 g and were 120 mm in length, 32 mm in diameter and had a 185 mm antenna. A PSAT was attached externally to each Atlantic salmon individual by bridling the tag to two cushioned back-plates. Back-plates were wired through the dorsal musculature below the dorsal fin with two biocompatible plastic-coated stainless steel wires. The inside of these plates had been surfaced with biocompatible silicon pads to reduce skin abrasion. A multifilament nylon thread attached each plate to the PSAT so that the PSAT streamed ≈1-2 cm behind the dorsal fin. PSATs were programmed to pop-up: at a specified date (in most cases after 156 days at sea), or if the PSAT crossed a maximum depth threshold (1200 m) to prevent tag destruction from high water pressure, or registered a constant depth. Although PSATs recorded depth and temperature data at short intervals (≈1-2 minutes), bandwidth limitations of data transmission to satellite after pop-up allowed only a 15 minute, or coarser, temporal resolution. PSATs had their position of pop-up registered by the ARGOS satellite positioning system. The limited battery life of PSATs precluded their use for long-term (>1 year) study.

DSTs (Star-Oddi Ltd) were 39 mm long and 13 mm in diameter, and had a mass of 9.2 g. DSTs measured depth and temperature at a constant interval (1-30 minute depending on the tag) over a long-term period (>1 year). Each DST was inserted to the peritoneal cavity according to the method described in Rikardsen and Thorstad (2006). Recaptures in the DST program were dependent on fishers. An information sheet was sent to fishers in the fjords and attached rivers before the commencement of the fishing season each year explaining how to return the tag, with a reward of 1200 NOK (≈140 USD) for successful return.

PSAT time-series were examined to identify if tagged Atlantic salmon had died due to predation or another reason. Adult Atlantic salmon at sea are eaten by whales (*Cetacea* spp.), seals (*Phocidae* spp.), sharks (*Selachimorpha* spp.), Atlantic bluefin tuna (*Thunnus thynnus*), skates (*Rajidae* spp.) and Atlantic halibut (*Hippoglossus hippoglossus*) (Joyce et al. 2002, Rikardsen et al. 2008, Lacroix 2014). As these species have depth use and diving patterns that differ from Atlantic salmon, predation could be identified from an abrupt change in depth and diving pattern from that of Atlantic salmon. Temperatures indicative of the tag passing through the alimentary canal of an endothermic predator also indicated predation. A continuous reading of the tag at the sea bottom was taken to indicate that the Atlantic salmon individual was dead. PSAT data recorded after the identification of such a death point were removed from further analysis.

To avoid the data sampling interval causing bias in our analyses of behaviour, tag data were divided into two categories: low (≥10 min) and high resolution (1 or 5 min). Both low and high resolution data were used for comparison of depth use patterns among the populations (Orkla, Alta and Neiden). High resolution data available for 13 Alta Atlantic salmon tagged with DSTs were used in a more detailed analysis of their diving behaviour. Low resolution data were not used to analyse diving behaviour because of the potential to not record short dives. Diving behaviour was examined only for individuals tagged with small internally implanted DSTs to reduce the potential for introducing behavioural bias in diving behaviour which may be associated with large external PSATs (see Hedger et al. 2017).

Comparison of populations (Orkla, Alta and Neiden)

To evaluate if there were differences in maximum diving depth according to where the Atlantic salmon from the three populations had migrated, the maximum depth recorded leading up to pop-up (from the day of and day preceding pop-up) of the PSATs was compared with the water column depth at the site of pop-up. Water column depth at the site of pop-up was determined by cross-referencing the location of the tag (determined by ARGOS satellite positioning) with the water column depth of that location, obtained from GEBCO – General Bathymetric Chart of the Ocean. Based on a maximum swimming distance of ≈50 km d^{-1} (see Lacroix 2013), the maximum fish depth recorded on the day of and day preceding pop-up will have occurred within 100 km of the position measured using the ARGOS system.

The depth distributions of the three populations were examined for temporal trends. Firstly, the depth frequency distribution, median, and maximum depth of Atlantic salmon from the three populations were examined for monthly changes. Hourly depth frequency distributions of the populations were examined seasonally for May – July (approximating polar day), August – October (the months between polar day and polar night), and November – January (approximating polar night)

Diving behaviour of Alta Atlantic salmon tagged with high resolution DSTs

Mean absolute vertical velocity (vertical distance moved between tag depth registrations over tag registration interval) was calculated as a function of hour of day for three times of the year: May – June (polar day for the latitude of the Alta River), August – October (the months between polar day and polar night), and November – January (polar night).

Dives below the euphotic zone (>200 m depth) were examined with regard to diving and surfacing velocities, maximum diving depth, time length of dive and change in temperature experienced. All dives (>25 m) and deep dives (> 200 m) were examined on a monthly basis to determine if there were long-term trends in relation to stratification, which could be indicative of a change in the availability of food. Stratification of the water column was defined as the depth of the mixed layer, as determined from the operational *TOPAZ4 Arctic Ocean system* (data provided by the *Copernicus Marine Environment Monitoring Service*). The relationship between the depth of all dives (>25 m) and the depth of the mixed layer was determined using a Generalised Estimation Equation (GEE) model (R function geeglm(geepack library)), with clustering of data according to individual.

RESULTS

Atlantic salmon migrated away from the coast to deep waters, as shown by the location of pop-up of PSATs (Figure 1). Of all PSATs for which data could be recovered (n = 66 out of 73 fish released, 90%), 47 (71%) popped-up due to constant pressure, 15 (23%) on the pre-set pop-up date, three were recaptured, and one measured a depth exceeding maximum threshold. Pop-ups resulting from a registration of a constant depth or a depth greater than the maximum threshold occurred in 50% of the Orkla PSATs releases, 67% of the Alta PSAT releases and 100% of the Neiden PSAT releases. Pop-ups occurred from the end of May, several weeks after release, until April the following year: no seasonal differences for time of pop-up were apparent for the Orkla or Neiden populations; however, the Alta population showed greatest numbers of pop-ups in November and December. Recovery rates for DSTs, indicative of a return from the sea and recapture, were 5.2% and 6.1% for Orkla and Alta Atlantic salmon respectively.

Recovered data for both individuals tagged with PSATs and individuals tagged with DSTs showed that the Atlantic salmon were pelagic, with occasional short forays into the water column. Atlantic salmon spent a mean of 81.6% of the time at depths <10 m (SD = 11.8%, min = 20.8%, max = 99.9%, n = 104 fish) and a mean of 87.8% of the time at depths <25 m (SD = 10.4%, min = 20.8%, max = 100%, n = 104 fish). Atlantic salmon spent the vast majority of time within the euphotic zone (<200 m depth) (mean = 98.6% of the time, SD = 1.41%, min = 94.4%, max = 100%, n = 104 fish). Thirteen individuals (out of 104) did not dive deeper than 100 m and 26 did not dive deeper than 200 m. The greatest depth recorded for individuals from the Orkla River was 610.6 m (SD = 221.3, min =17.5, n = 13 fish), 706.7 m (SD = 178.3, min = 14.1, n = 77 fish) for the Alta River and 347.0 m (SD = 113.1, min = 21.5, n = 14 fish) for the Neiden River.

Comparison of populations (Orkla, Alta and Neiden)

The Atlantic salmon from the different populations migrated to different areas (Figure 1), which appeared to influence the likelihood of deep dives. Pop-ups from the Orkla population mainly occurred in the western Norwegian Sea around the Mid-Atlantic ridge between

Iceland and Svalbard. Pop-ups from the Alta population occurred in two regions: (i) along the Mid-Atlantic ridge, nearer to Svalbard than Iceland and (ii) in the Barents Sea. Pop-ups from the Neiden population occurred in the Barents Sea, with the exception of two individuals that migrated northward to Svalbard. Near the time of pop-up (day of and day preceding pop-up), dive depths depended on geographical location. Individuals within the Barents Sea (east of 15^{o}E) dived to significantly greater depths (median = 120 m, min = 0 m, max = 519 m, n = 31) than those in deeper waters, offshore in the Norwegian Sea (west of 15^{o}E) (median = 2 m, min = 0 m, max = 196 m, n = 20) (Wilcoxon rank sum test, W = 211, p = 0.028).

Long-term (monthly) and short-term (diurnal) trends in depth use were evident in all three populations. Atlantic salmon from the Alta and the Orkla spent more time at depths >5 m during the summer months of July to October, less during the autumn/winter months of November to February, and then more again during the spring months of March to May (Figure 2, upper panels). Individuals from the Neiden population only provided data until January following release, but showed a similar pattern of greater occupancy of depths >5 m during summer than winter. Median depths were mostly within the upper 10 m of the water column, but a seasonal trend was present, with shallower median depths immediately after sea entry (May) and during winter (December-February) than in summer, followed by a return to deeper median depths (for the Alta and the Orkla individuals) in the following spring (Figure 2, middle panels). Dive depth increased as the Atlantic salmon migrated away from their release points, and Orkla and Alta individuals typically dived to 100-200 m from March the year after release (Figure 2, lower panels).

Diurnal patterns in depth use depended on time of year (Figure 3). In the first few months after release (May – July, where there was polar day at high latitudes), there was no diurnal trend in depth use. However diurnal trends were evident later (August – October, where there was a mixed daytime/night-time regime),with greater depths being registered from 6:00 – 18:00 Hrs than from 18:00 – 1600 Hrs (as measured by the clock, calibrated to the position of release). Even later (November – January, where there was polar night at high latitudes), this diurnal behaviour was apparent, but the period of use of greater depths was confined to a shorter number of hours during the day. Diurnal behaviour from November to January was weakest for individuals from the River Alta.

Diving behaviour of Alta Atlantic salmon tagged with high resolution DSTs

Vertical movements were greater during day than night (Figure 4), however, the tendency to diurnal patterns was strongly dependent upon time of year. During times approximating the polar day and polar night for the latitudes of the River Alta and northwards, there was a much weaker diurnal pattern than during the season between polar day and night. When Atlantic salmon experienced a 24 hour day-night cycle, mean vertical velocities ranged from ≈0.5 m min^{-1} at 24:00 Hrs to ≈1.65 m min^{-1} at 12:00 Hrs (from the tag clock calibrated to position of release).

Visual inspection showed that most deep dives (>200 m) followed a ‘U’ shape (≈42.1% of deep dives) rather than a ‘V’ shape pattern, with an initial rapid descent, followed by a period of time lingering at depth and concluding with a rapid ascent to the surface (Figure 5a). Diving velocities were ≈0.5 m s^{-1} near to the dive’s initiation and declined to 0 m s^{-1} over a period of ≈20-30 minutes as the trough of the dive was approached. There was typically little vertical movement at depth until the individual accelerated towards the surface to finish the dive. Some dives showed a skewed ‘U’ shape in which there was a slight surfacing trend before the individual rapidly swam towards the surface (≈22.2% of deep dives) (Figure 5b). A smaller number of dives showed a ‘U’ shape in which the individual dived with an initial rapid descent, before a slow approach of the trough of the dive (≈7.6% of total dives). Other dives showed more complex patterns. Firstly, some dives were generally ‘U’ shaped but involved multiple short-term vertical movements around the trough of the dive (≈22.0% of total dives) (Figure 5c). Other dives involved occupancy of a distinct sill depth, where the individual remained for an extended time before or after the individual dived to deeper depths (≈6.2% of total dives) (Figure 5d).

Overall, the descending phase was significantly faster than the ascending phase (Wilcoxon signed rank test, $V = 91$, $p < 0.001$, $n = 13$ fish) (Figure 6a). The mean of individual descent velocities was 0.20 m s^{-1} (range = 0.11-0.35 m s^{-1}, $n = 13$ fish), and on ascent 0.10 m s^{-1} (range = 0.05-0.18 m s^{-1}, $n = 13$ fish). The proportion of deep dives was inversely proportional to the dive depth, with only 1.8% of dives to >600m depth (Figure 6b). Deep diving events lasted for several hours (median time = 2.31 h, range = 0.18-22.5 h, SD = 2.03 h) (Figure 6c). Diving typically involved relatively small decreases in temperature (median = 0.4ºC, max = 5.8ºC) (Figure 6d).

Deep diving events were aperiodic and the time between successive deep dives was highly positively skewed, with more than 20% of surfacing events from a deep dive followed by a subsequent deep dive less than 15 mins later. However, a similar percentage of surfacing events involved the individual staying at the surface for more than two days, and one individual went for 74 days between deep dives. Some individuals occasionally spent long periods on the surface without performing deep dives, followed by multiple successive deep dives. Atlantic salmon exhibited both shallow and deep dives throughout the year, but the overall diving pattern was associated with changes in the mixed layer depth (Figure 7a). When the mixed layer was near to the surface (depth <50 m, June – October), most dives were relatively shallow. When the depth of the mixed later increased (depth 150 – 250 m, mid-November – May), dives tended to be deeper. Diving depth (Figure 7b) increased with the depth of mixed layer (GEE, $p < 0.001$, cluster $n = 13$). The diving rate showed a similar seasonal pattern. The rate of all dives >25 m was strongly related to time of year, with diving rate being greatest in summer (peaking in August and September), and lowest during winter (reaching a minimum in December) (Figure 7c). In contrast, the rate of deep dives (>200 m) was greater during winter (when the mixed layer depth had deepened) than during summer.

DISCUSSION

This study has used two different tag types – PSATs and DSTs – to elucidate diving behaviour in tagged Atlantic salmon individuals from three populations. The use of the different tag types was not consistent among the populations, with ≈71% (Orkla), ≈55% (Alta) and 100% (Neiden) of individuals being tagged with PSATs rather than DSTs. Given this, it is necessary to consider the potential for tag effects to bias results of the study. Hedger et al. (2017) showed that although depth distributions among Atlantic salmon individuals tagged with PSATs were broadly similar to those of individuals tagged with DSTs, those tagged with PSATs tended to dive to shallower depths and dived less frequently than those tagged with DSTs. This may have slightly biased our estimates of overall depth distributions when comparing populations. However, the consistency in seasonal trends in depth behaviour among populations in the current study suggests that a mix of tags may still be applied effectively to compare populations. For analysis of environmental influences on diving behaviour, the current study focused on the high resolution DSTs, so differential tag effects were not an issue.

Consistency among populations

Atlantic salmon from the three populations showed similar depth use and diving patterns during their marine migration. Firstly, all populations showed a trend of increasing use of subsurface waters (depth >5m) from release until later summer (August), followed by a return to greater occupancy of surface waters in winter (December – February). Secondly, all populations showed similar changes in diurnal patterns, with no diurnal variation during May – July, and increased use of greater depths during daytime in August – October. During November – January, Orkla and Alta populations showed little diurnal pattern, whereas there was more use of greater depths for ≈4 hours around 12:00 Hrs (using the tag clock calibrated to position of release) for the Orkla population.

Although the Atlantic salmon came from three different populations, they were migrating to waters similar in terms of surface temperature and depth of the mixed layer, so it is not that surprising that they showed similarities. In comparison, stocks of North American Atlantic salmon have shown different diving patterns (Reddin et al. 2011, Lacroix 2013, Strøm et al. 2017) which may be related to differences in environmental conditions between the current study and those conducted in North American locations.

Trends in depth use and diving among populations

Atlantic salmon behaviour in the initial phase of sea migration was not dominated by deep dives. There was little diving in the first month after release despite the fact that fjord and coastal zone depths could exceed several hundred metres. This is consistent with results from previous studies of Atlantic salmon kelts and post-smolts, both in the North West Atlantic and the North East Atlantic, showing swimming through the near surface layers with a lack of deep diving (LaBar et al. 1978, Davidsen et al. 2008, Halttunen et al. 2009, Gudjonsson et al. 2015). Diet studies of Atlantic salmon in the fjords of this study show that Atlantic salmon post-smolts feed almost exclusively on fish (Rikardsen et al. 2004). Post-smolts of other salmonids – Arctic charr (*Salvelinus alpinus* L.) and sea trout (*Salmo trutta L.*) – in the Altafjord have been found to feed pelagically on herring (Rikardsen & Amundsen 2005) when the prey was abundant. Given that adult Atlantic salmon in the current study were in poor condition on first entering the sea (median condition factor (K) = 0.74), it can be expected that they would have had the impetus to feed. Thus we propose that they were feeding pelagically in the first month at sea during the transit away from the coast when prey were available.

Further from release, some individuals did show occasional dives (depths of 200 – 400 m) in summer (June – August) (Supplementary figure 1). This is suggestive of them having moved off the continental shelf into the Norwegian Sea. Lacroix (2013) observed deep dives when post-spawners crossed the deep Laurentian Channel or migrated to the edge of the continental shelf, and hypothesised that they may have been looking for a thermal refuge or orientation cues, or feeding in highly productive upwelling water at the continental shelf edge. Given that deep dives at this time were rare occasional events, we hypothesise that this is an example of exploratory and orienteering behaviour rather than foraging behaviour, triggered by the Atlantic salmon moving from coastal to deeper waters.

In the winter and spring following release, the Atlantic salmon behaviour changed to deep diving. Greater maximum depths were observed for all populations in winter, and for the Orkla and Alta individuals tagged with DSTs that had extended coverage into the spring. In addition, the frequency of deep diving increased for the Alta Atlantic salmon tagged with high-resolution DSTs. Atlantic salmon in the deep sea have been shown to feed on the mesopelagic community, both in the NW Atlantic (Lear 1972) and the NE Atlantic (Hansen & Pethon 1985). This may be the cause of the deep dives shown in the current study. Near the time of pop-up, Atlantic salmon which had migrated to the deeper part of the Norwegian Sea (from the Orkla and one-third of the Alta population) dived within the water, but to shallower depths than those that migrated to the shallow Barents Sea (from the Neiden and two-thirds of those from the Alta population). Differences in diving depths may indicate different feeding behaviours. Prey fish for adult Atlantic salmon, including herring, capelin (*Mallotus villosus*), and sand eel (Haugland et al. 2006, Rikardsen & Dempson 2011, Renkawitz et al. 2015), are found throughout the Norwegian and Barents seas (see Jakobsen & Ozhigi 2011), but there is limited information on how their distributions change spatially and temporally, so it is difficult to relate the diving behaviours of Atlantic salmon in these seas to differences in prey availability. Some of the deep dives within the Barents Sea preceding pop-up were deep enough that they may have been diving to the sea bottom, so the Atlantic salmon could also have been feeding on benthic related prey items. However, the ability for Atlantic salmon to quickly migrate allowed for the possibility that they could have been diving in deeper waters before a pop-up took place at a relatively shallow location.

Environmental influences on diving

Short- and long-term changes in the depth frequency distribution of all populations, and in the vertical velocities of the Alta Atlantic salmon tagged with high resolution DSTs, are likely associated with changes in light. Adult Atlantic salmon at sea have been shown to dive more during daytime than night-time and/or occupy nearer surface waters at night-time (Holm et al. 2006, Reddin et al. 2011, Renkawitz et al. 2012, Lacroix 2013). Atlantic salmon from all rivers in the current study showed a diurnal pattern of depth occupancy, that was attenuated during polar day and polar night. Depth did not change according to hour of day from May to July, during the polar day. Thus, the lack of diurnal changes in depth use during this period may be related to the small diurnal variation in light intensity. Later in the year (August – October), periods of night-time began to return, which was associated with increased use of greater depths during daylight. Later in the winter (November – January), PSAT data suggest that Atlantic salmon from all three populations were in northern latitudes. During this time, both the length of daylight and twilight were short, which were associated with shorter periods (≈4 hours) of use of greater depths for the Orkla and Neiden Atlantic salmon. When the daytime lasted a short period, the greatest depth use of Neiden Atlantic salmon occurred 4 hours earlier than noon at the local time of the River Neiden (for which the tag clock was set). Therefore, if they were diving during the brightest conditions around noon during the short winter day it is likely that Neiden Atlantic salmon had moved ≈60^{o} east of the release site. Of the three populations, the Alta Atlantic salmon had the least difference in depth according to time of day during winter. This suggests that the Alta Atlantic salmon were at latitudes with smaller daily differences in light intensity i.e., were farther north. The Alta Atlantic salmon tagged with high resolution DSTs showed a similar pattern. Vertical movements for the Alta Atlantic salmon were greatest in August – October when there was greatest diurnal contrast in illumination. These vertical movements would be consistent with visual foraging during the daytime period.

Diurnal variation in depth use by Atlantic salmon may be directly affected by variation in light conditions by creating opportunities for visual foraging. Indirect effects of light are also possible if they feed on prey that have diurnal vertical migrations. Atlantic salmon are able to feed in the dark, as evident from them feeding in darkness under ice cover (Finstad et al. 2004). However, foraging would likely be more efficient if they can use their visual sense. Therefore, the depth at which Atlantic salmon feed may be a function of prey location and relative visual feeding efficiency. If most prey were deeper in the water column, occupancy of greater depths would be expected during brighter periods of the day (see Reddin et al. 2011), when Atlantic salmon can use their vision to forage which would concur with the seasonal/diurnal depth patterns observed in this study.

Diving behaviour was probably not related to suboptimal summer or winter thermal conditions. Reddin (2011) proposed that during stratification in summer Atlantic salmon dived for short periods of time to catch prey despite cold suboptimal conditions and return to the surface to digest prey. Lacroix (2013) hypothesised that adult Atlantic salmon avoided the surface layer in the Labrador Sea during winter because supercooling caused surface temperatures to fall below a critical threshold of -0.76 ^{o}C (see Saunders 1986, Fletcher et al. 1988). However, neither of these conditions were observed in our study. It was rare for a Atlantic salmon to dive into temperatures below the critical threshold, and the temperature change during dives was not great, with ≈87% of dives never involving a reduction in temperature of >2^{o}C. Median surface (depth <5 m) temperatures during winter (December – January) were 3.6, 4.3 and 5.2^{o}C for Orkla, Alta and Neiden populations, respectively, so Atlantic salmon were not experiencing supercooling near the surface. This was because variation between winter and summer in terms of sea surface temperature is less for the North

East Atlantic, where this study was based, than that for the North West Atlantic. Thus the difference between Atlantic salmon behaviour in this study and that of Reddin (2011) and Lacroix (2013) may be due to the different environments. It is also unlikely that diving behaviour was influenced by low oxygen levels in the mesopelagic. Hypoxia in Atlantic salmon occurs at dissolved oxygen (DO) levels below 6 mg l^{-1} (Burt et al. 2013). Predictions by the *TOPAZ4 Arctic Ocean Biogeochemistry Analysis and Forecast* always showed DO levels greater than 8 mg l^{-1} throughout the mesopelagic in the Norwegian and Barents Sea, so Atlantic salmon in the current study were not diving into conditions likely to induce hypoxia.

Changes in the frequency and diving depth of Alta Atlantic salmon tagged with high resolution DSTs coincided with changes in stratification, with frequent shallow dives during near-surface stratification, and a reduction in the rate of shallow dives but an increase in the rate of deep dives when the mixed layer extended to a depth of several hundred metres. Diving has been related to stratification in other marine fishes. Waller et al. (2009), for example, found that Atlantic bluefin tuna showed preference for surface layers when in strongly stratified waters, spent less time above the thermocline when in weakly stratified waters, and dived to depths that were positively related to the depth of the thermocline. They speculated that strong thermal stratification may facilitate prey detection and improve the chance of successful feeding. Atlantic salmon in the current study dived to deep waters only after a relatively long period at sea. The delay may be related to the deepening of the mixed layer, and consequent changes in prey aggregation. Deep (>200 m) diving exhibited by Alta Atlantic salmon with high-resolution DSTs was characterised by relatively infrequent and short duration ‘U’-shaped dives. These ‘U’ shaped dives have been hypothesised to be indicative of foraging behaviour in bluefin tuna (Wilson & Block 2010), and this may be the case for the adult Atlantic salmon in the current study.

CONCLUSION

Diurnal and seasonal patterns in depth use and diving were broadly consistent among groups of tagged Atlantic salmon in the northern part of the North East Atlantic. This was manifested as use of greater depths during daylight on a daily time scale. Seasonally, this involved use of deeper depths in summer, more use of nearer-surface depths at the onset of winter, and a return to more use of deeper depths in late winter and spring with a concurrent increase in deep dives (>200 m) into the water column. The diurnal effect was likely associated with changes in light-regime, as suggested by transitions in behaviour between polar day and polar night. The seasonal pattern of deep diving may have been influenced by seasonal trends in the depth of the mixed layer, which we hypothesise affects diving behaviour by aggregating sources of prey.

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TABLES

Table 1. The Atlantic salmon from the Orkla, Alta and Neiden Rivers tagged with pop-up satellite archival tags (PSATs) and data storage tags (DSTs). n = sample size. High and low temporal resolution DSTs are shown by H and L suffixes respectively. For Atlantic salmon body length and body mass, ranges are shown in parentheses.

Population	Orkla		Alta			Neiden
Tag type	PSAT_L	DST_L	PSAT_L	DST_L	DST_H	PSAT_L
Release						
Years	2010	2010	2008-2010	2008-2012	2013-2015	2009-2010
No	10	57	47	348	229	16
Mean body length (cm)	98 (88-114)	89 (71-107)	99 (92-112)	92 (57-114)	87 (56-112)	91 (73-107)
Mean body mass (kg)	6.7 (4.7-9.8)	4.8 (2-6-9.0)	7.2 (5.4-9.9)	6.0 (1.4-13.0)	5.2 (1.2-1.1)	5.4 (2.8-9.8)
Recovered						
No	10	3	42	22	13	14
Mean data length (d)	147	415	135	407	411	104
Mean body length (cm)	98 (88-114)	90 (87-94)	99 (92-112)	92 (80-104)	92 (79-99)	92 (73-107)
Mean body mass (kg)	6.7 (4.7-9.8)	4.9 (4.5-5.5)	7.3 (5.4-9.9)	6.0 (4.0-9.0)	5.4 (3.2-6.7)	5.7 (2.9-9.8)
Median recording interval (min)	15 (n = 3) 30 (n = 7)	30 (n = 3)	15 (n = 18) 30 (n = 13) 45 (n = 1) 60 (n = 10)	2 (n = 10) 30 (n = 20)	1 (n = 7) 5 (n = 6)	15 (n = 7) 30 (n = 4) 60 (n = 3)

FIGURE CAPTIONS

Figure 1. Study area showing positions at pop-up (circles) of PSATs that had been attached to Atlantic salmon from the Orkla (green), Alta (red) and Neiden (yellow) Rivers, with places of release (triangles).

Figure 2. Depth use of all tagged Atlantic salmon from the Orkla, Alta and Neiden Rivers according to month from release: percentage depth frequency distribution (upper panels), median depth (middle panels), and maximum depth (lower panels). Data from the Neiden tag-group were not available after January the year after release. Percentage depth frequency distributions are determined for each salmon individual, and a mean of individual percentage frequency distributions is shown. Median and maximum depths were determined on a daily basis, and the means of these calculated per month are shown. Numbers of individuals used in the estimate are shown above each bar.

Figure 3. Percentage depth frequency distribution of tagged Atlantic salmon from the Orkla, Alta and Neiden Rivers according to hour of day for May – July (upper panels), August – October (middle panels) and November – January (lower panels). Hour of day is calibrated to the position of release. Percentage depth frequency distributions are determined for each salmon individual, and a mean of individual percentage frequency distributions is shown. The actual time of day experienced by the salmon will be offset by this by +1 hour for every 15^o the individual moves eastward and -1 hour for every 15^o westward.

Figure 4. Absolute vertical velocity of 13 Atlantic salmon from the River Alta carrying high temporal resolution DSTs according to hour of day for May – July, August – October, and

November – January. Hour of day is that recorded using a clock calibrated to the position of release.

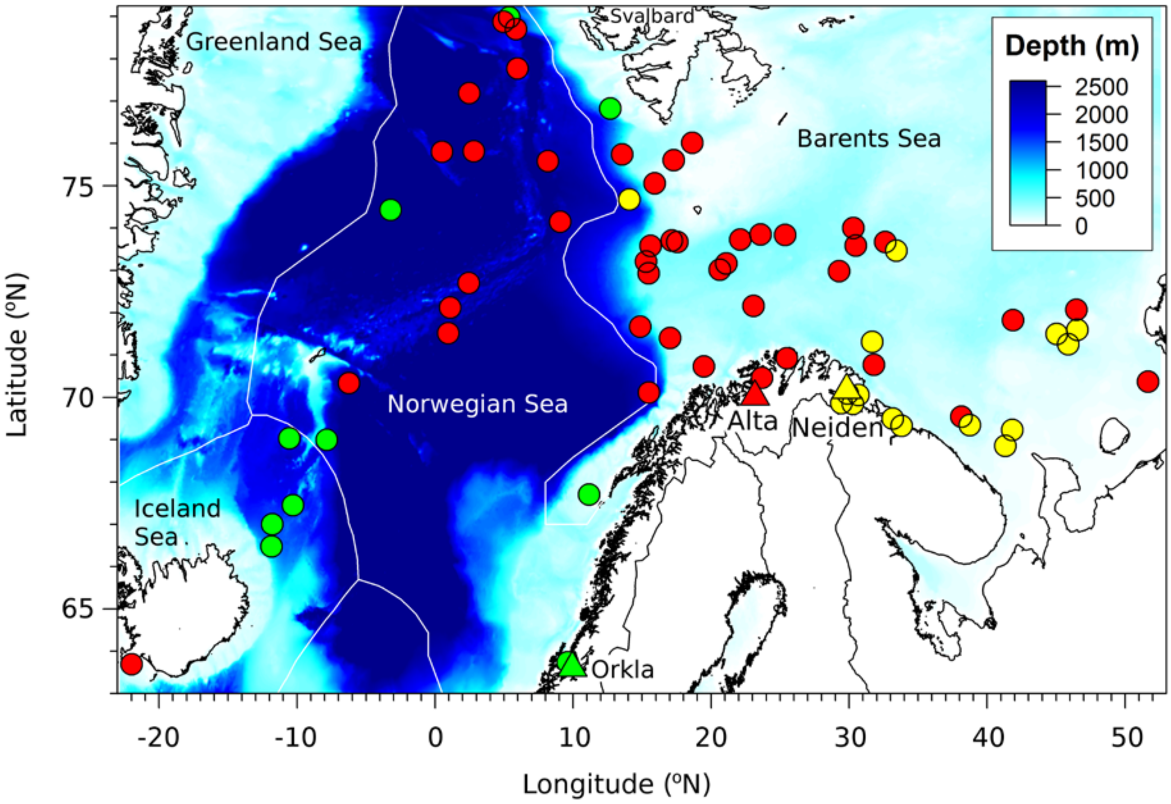
Figure 5. Deep dive characteristics (>200 m) for selected Atlantic salmon from the River Alta carrying DSTs: (a) ‘U’ shaped pattern; (b) skewed ‘U’ shape pattern; (c) movement to depth with multiple depth fluctuations before surfacing; and (d) movement to depth followed by sustained presence as a shallower depth before surfacing. Positive diving velocities indicate the descending phase, and negative diving velocities indicate the ascending phase.

Figure 6. Characteristics of the deep dives (>200 m) by 13 Atlantic salmon from the River Alta carrying high temporal resolution DSTs: (a) diving velocity; (b) maximum depth; (c) length of dive; and (d) difference between surface and trough (maximum depth) temperatures.

Figure 7. Long-term trend of diving behaviour of 13 Atlantic salmon from the River Alta carrying high temporal resolution DSTs: (a) depth and temperature versus time; (b) median depth of dives where depth > 25 m; and (c) total number of dives (depth > 25 m) and number of deep dives (depth > 200 m). The depth of the mixed layer (solid line), calculated for a convex polygon encompassing all pop-up locations for these individuals, has been superimposed on (a) and (b) (obtained from the Operational Mercator Global Ocean Analysis and Forecast System through the Copernicus Marine Environment Service). In (b) and (c) numbers above each box show the number of individuals.

Supplementary figure 1. Depth and temperature versus time for 7 recovered Atlantic salmon from the River Alta tagged with high temporal resolution DSTs released in 2015. The depth of the mixed layer (solid line), calculated for a convex polygon encompassing all pop-up locations for the Alta salmon tagged with high resolution DSTs, has been superimposed (obtained from the Operational Mercator Global Ocean Analysis and Forecast System through the Copernicus Marine Environment Service).

FIGURES



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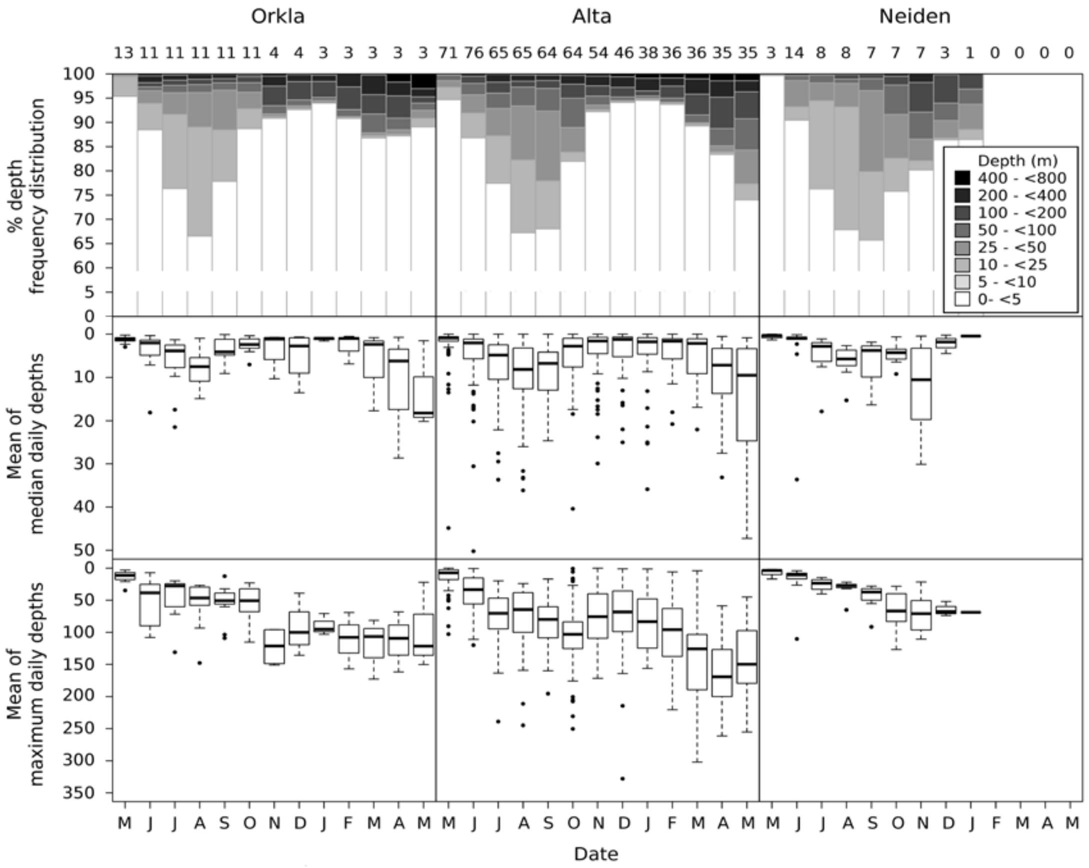

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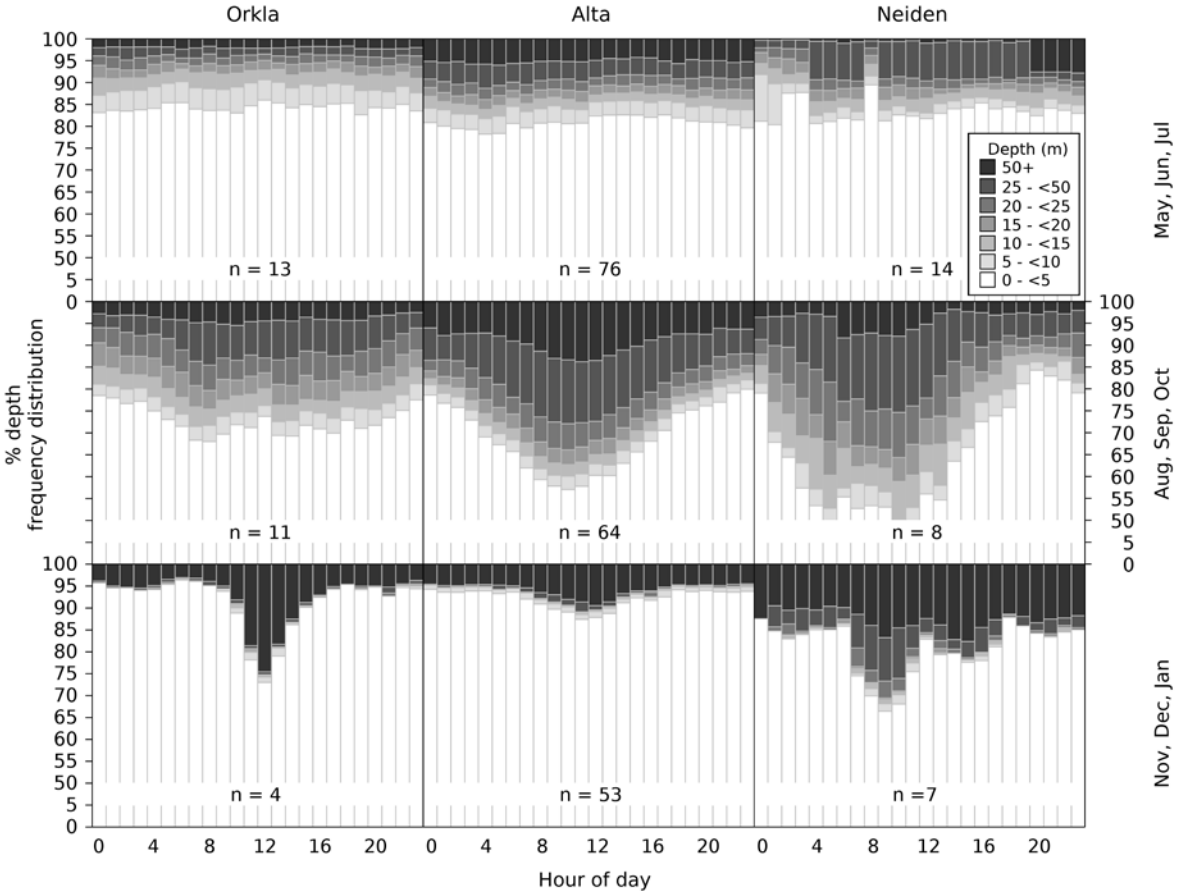

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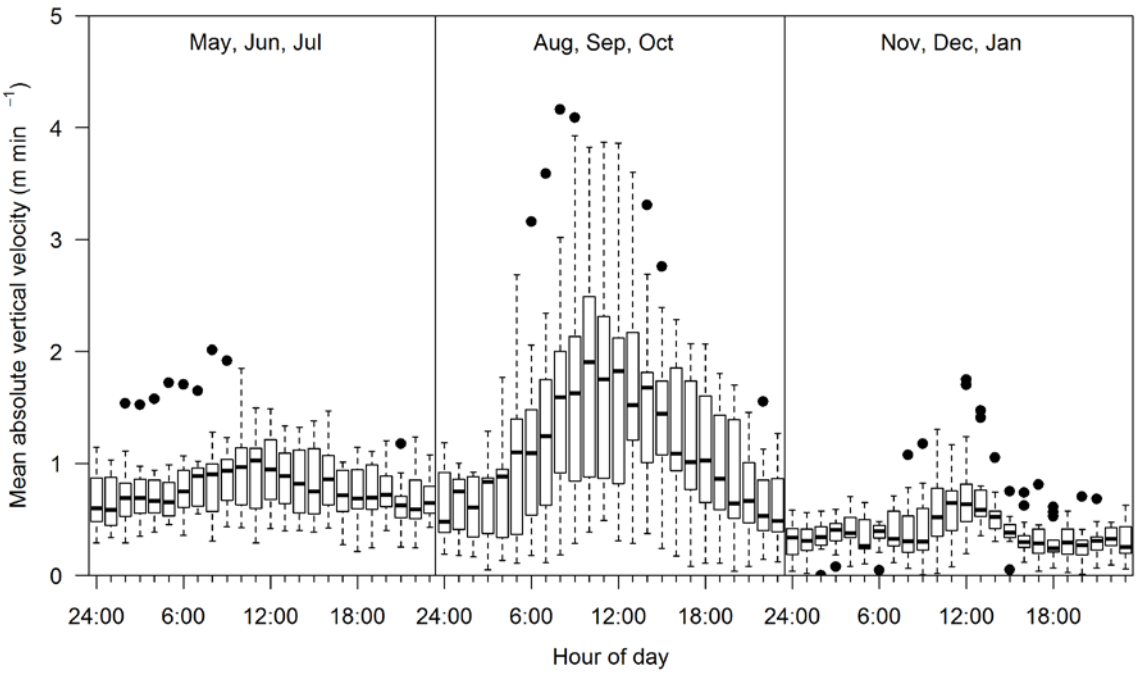

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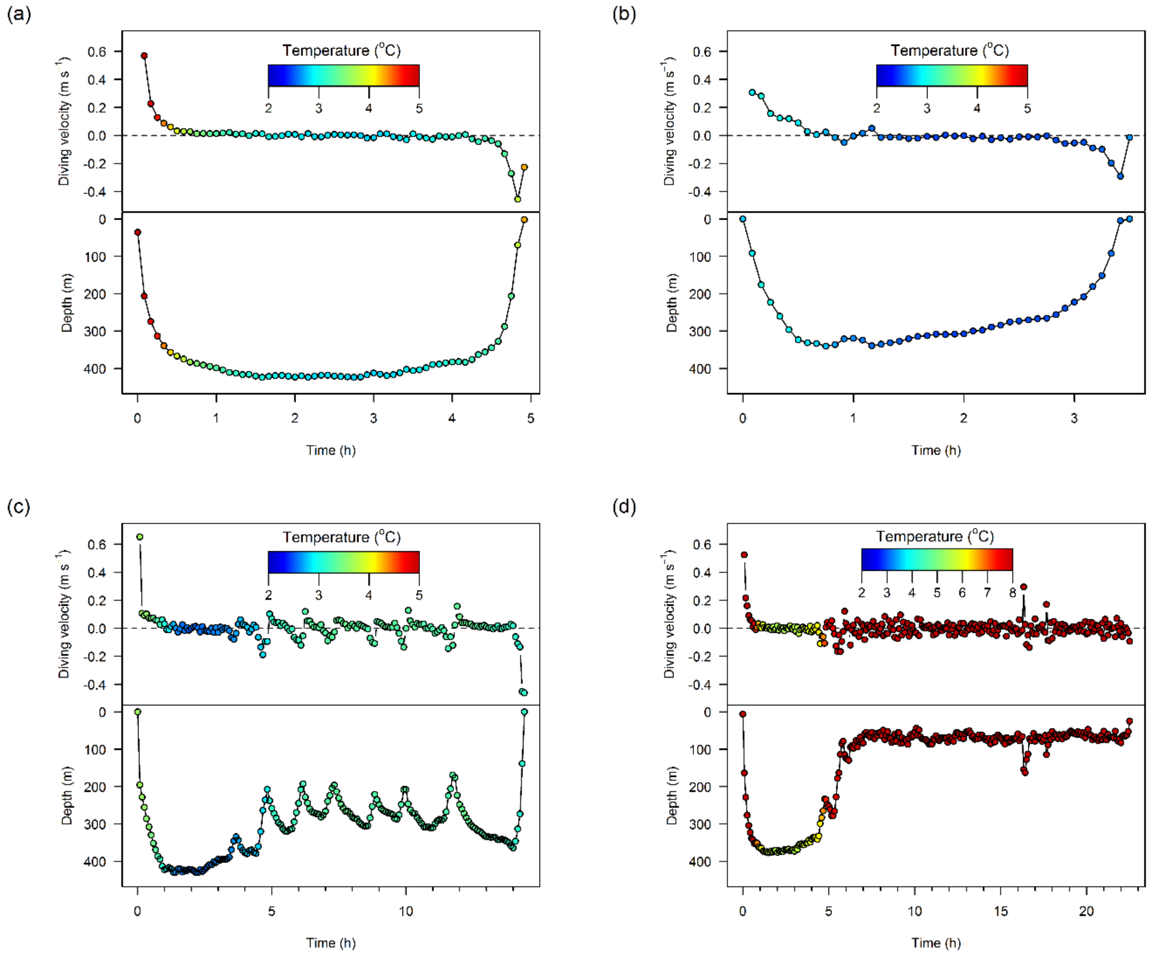

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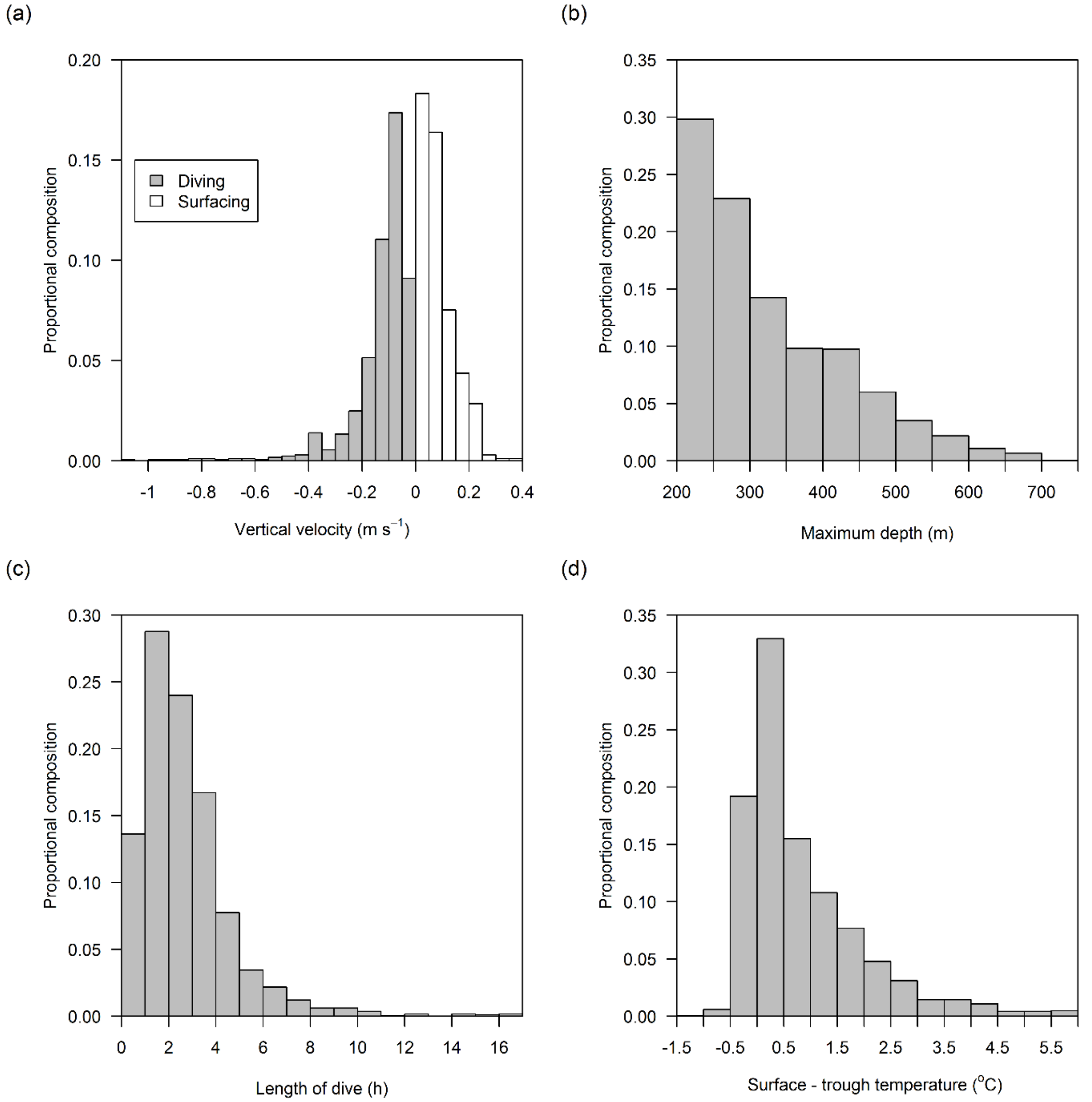

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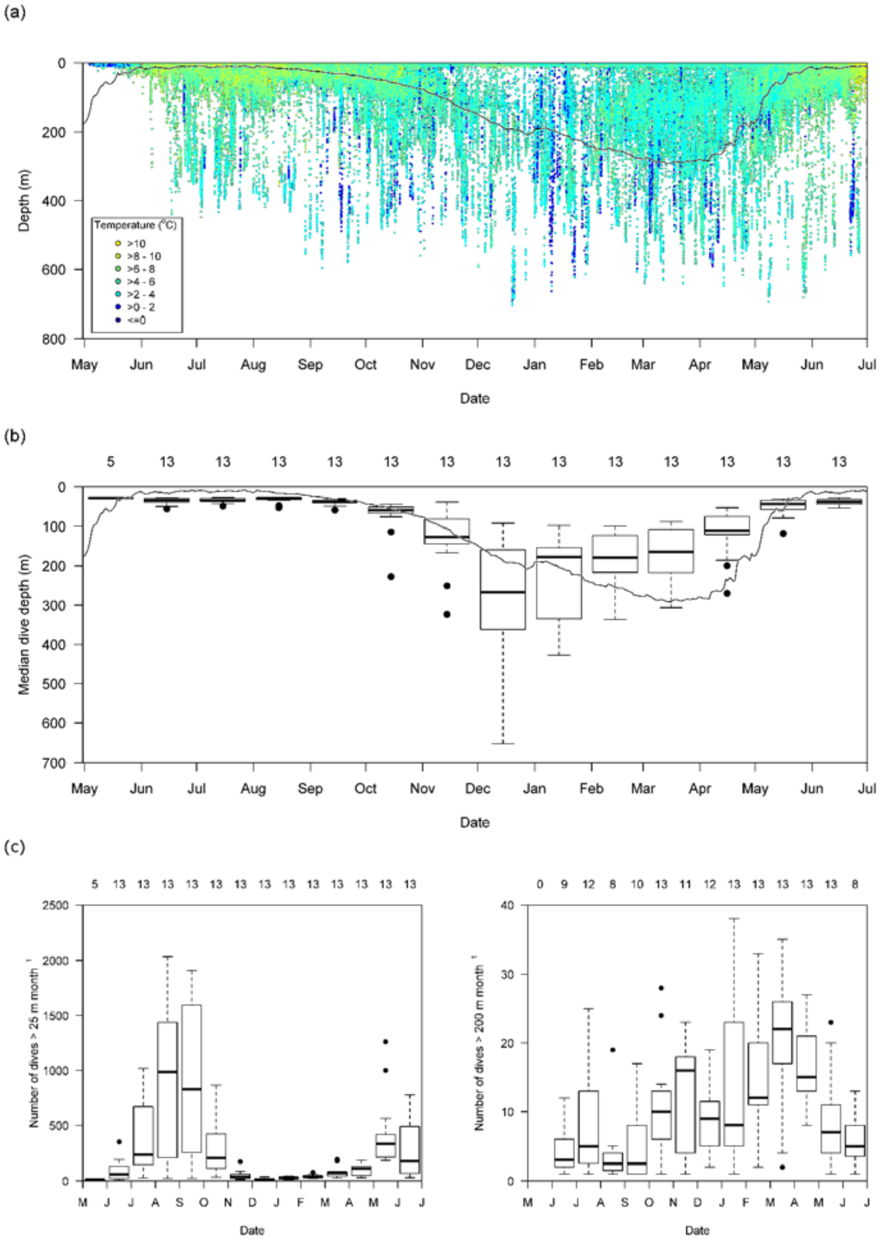

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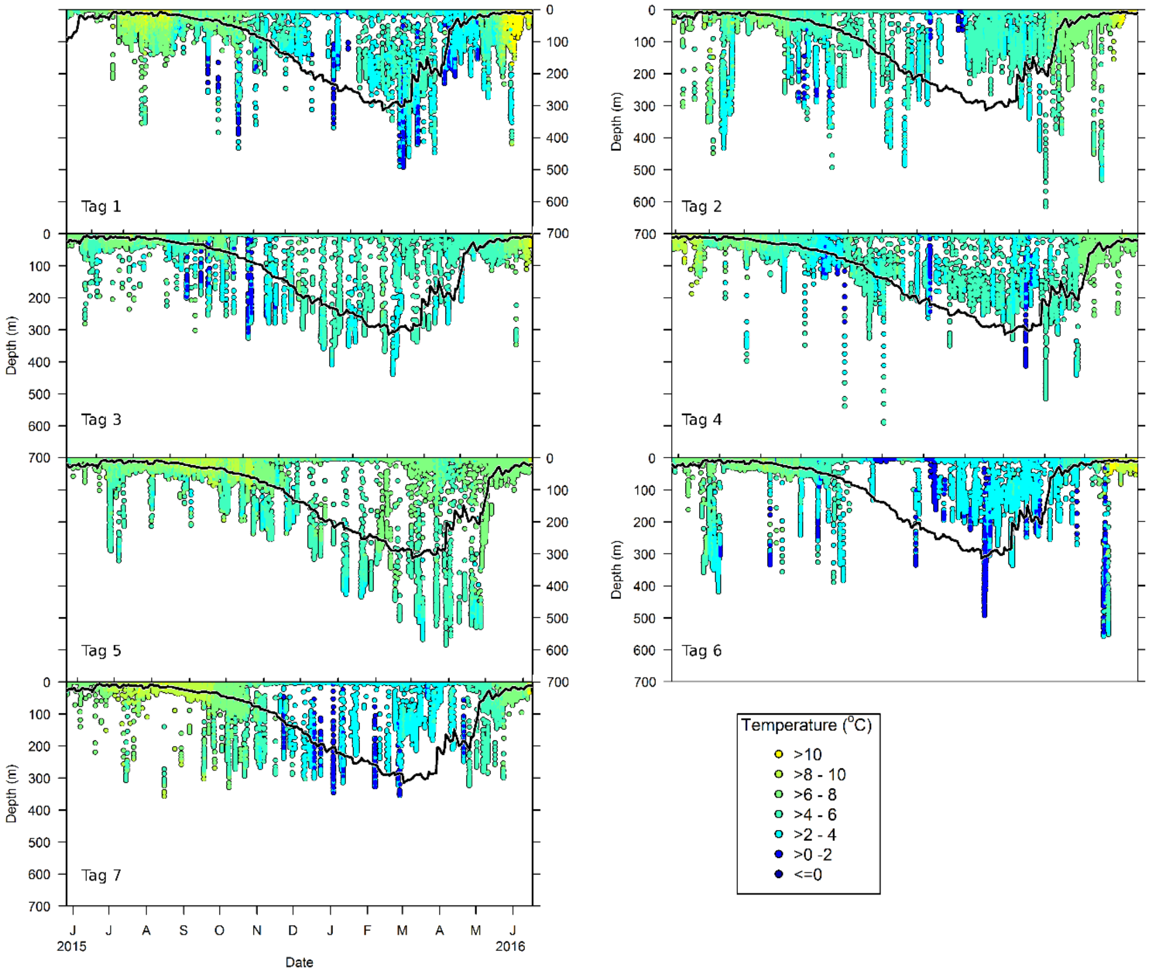
SUPPLEMENTARY FIGURES



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